THE UNIVERSITY OF ALBERTA

PALSAS IN BAKER CREEK BASIN N.W.T.: AN ECOSYSTEMATIC STUDY

by

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A THESIS

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ABSTRACT

Peatland (both minerotrophic and ombrotrophic) extends from southern Canada northward to include parts of the continuous permafrost zone. In the subarctic, discontinuous permafrost is restricted mainly to peatlands and often occurs as raised peat landforms termed palsas. Palsa uplift results from water migration to the freezing plane as well as buoyancy and water volume expansion upon freezing. The genesis of palsas (that form in minerotrophic topogenous carr peatlands) occurs in *Carex* - *Tomenthypnum* meadows where individual peat hummocks develop a perennially frozen core. Organic accretion and permafrost aggradation cause these hummocks to become larger and more numerous.

Surface peat of the larger hummocks is drier than surface peat of the *Carex* - *Tomenthypnum* hummocks. As a result, the *Betula* - *Pohlia* association becomes dominant. Over the years, permafrost aggradation coupled with slow peat infilling of depressions between hummocks results in a raised peat landform having a perennially frozen core.

Termed a palsa, the uplifted peat surface is drier than surface peat of the *Betula* - *Pohlia* hummocks. The dryness results in the dominance of the *Ledum* - *Cladonia* association as well as the climatic climax *Picea* - *Cladonia* association.

Environmental differences exist between plant associations. However, within each association the environment is uniform. Differing plant associations provide habitats of varying suitability for small mammals. Habitat suitability is greatest in the *Betula* - *Pohlia* plant association and decreases toward the climatic climax *Picea* - *Cladonia* association.

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CHAPTER ONE

INTRODUCTION

1.1 INTRODUCTION

Permafrost refers to the thermal conditions of earth materials when their temperature remains below $0^{o}C$ continuously for a number of years. It occurs where there is a negative heat balance and is defined exclusively by temperature. At the southern fringe of the subarctic, permafrost is restricted mainly to peatlands (Brown 1970) and often occurs in distinct raised peat landforms termed palsas. Palsas generally are less than 100 m in diameter and vary in height from 1 - 3 m (Sjörs 1961).

Palsas have attracted the interests of researchers in Europe (Rapp and Rudberg 1964, Mörnsjö 1968, Ruuhijarvi 1968, Salmi 1968, Schenk 1968, Svensson 1968, Lundquist 1969, Mörnsjö 1971, Wramner 1972, Warmner 1973, Sollid and Sorbel 1974, Vorren and Vorren 1975) and in North America (Sjörs 1959, Railton and Sparling 1973, Zoltai and Tarnocai 1971, Zoltai 1972, Thie 1974, Brown 1977, Reid 1977). Until the present study, however, no work has been available that analyzed palsa development within the Precambrian Shield of Canada or similar physiographic regions elsewhere.

1.2 PURPOSE OF RESEARCH

This study analyzes the interrelations of vegetation and physical environment that form palsas in a small area of the Canada Precambrian Shield. Palsa development is linked to plant succession, therefore seral

trends within the study area are examined. Individual successional associations function as habitat for small mammals, thus the influence of palsa formation on habitat development is analyzed. To understand these interactions I studied the geomorphology, microclimate, plant succession and small mammal distribution of three separate depressions near Yellowknife, Northwest Territories.

1.3 ECOSYSTEMATIC APPROACH

The ecosystematic approach is used in the present study to analyze and classify varying combinations of the physical environment as they interact with the flora of palsas to form small mammal habitat. The ecosystem concept has been used by many researchers to study the interaction of biotic communities with the physical environment (Stoddart 1965, Odum 1969, Gill 1972). Vegetation units formed by the plant-habitat complex are defined as plant associations. The association concept implies a uniform aggregation of plants which are in dynamic equilibrium with the physical environment. I used this concept to analyze the flora of the study area.

1.4 STUDY AREA

Research for the present study took place in the northeast sector of Baker Creek Basin, situated on the west side of Yellowknife Bay, between 62^{o} 28' and 62^{o} 43' north and 114^{o} 17' to 114^{o} 31' west (Figure 1). Intensive work was conducted between Oro and Chan Lakes (Figure 2).

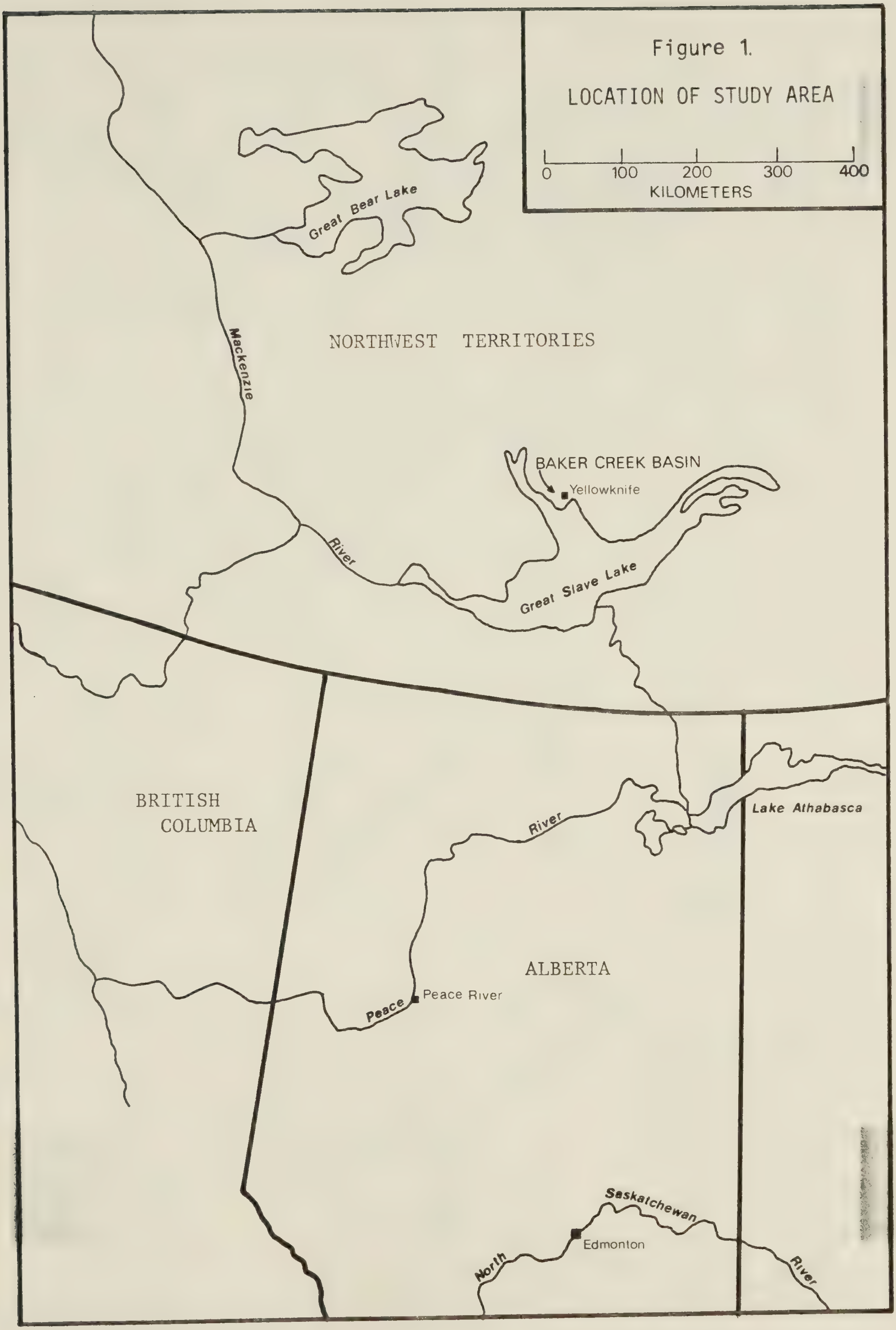


Figure 1.
LOCATION OF STUDY AREA
0
100
200
300
400
KILOMETERS
Great Bear Lake
Mackenzie
NORTHWEST TERRITORIES
BAKER CREEK BASIN
Yellowknife
River
Great Slave Lake
BRITISH COLUMBIA
River
Lake Athabasca
ALBERTA
Peace
Peace River
Saskatchewan
Edmonton
North
River

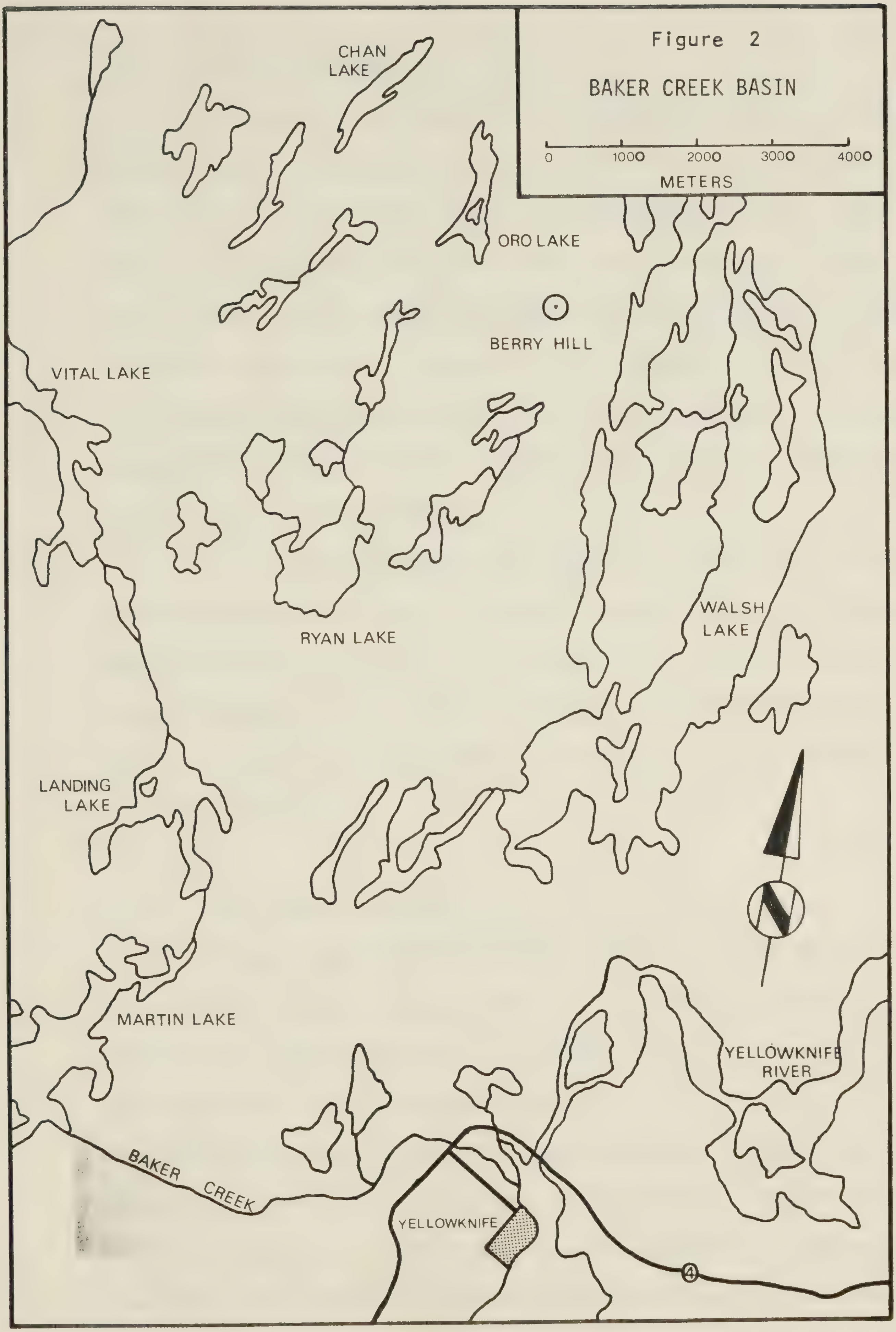


Figure 2
BAKER CREEK BASIN
0
1000
2000
3000
4000
METERS
CHAN LAKE
ORO LAKE
BERRY HILL
VITAL LAKE
RYAN LAKE
WALSH LAKE
LANDING LAKE
MARTIN LAKE
YELLOWKNIFE RIVER
BAKER CREEK
YELLOWKNIFE
N
4

1.4.1 STUDY AREA CLIMATE

Because of the study area's location, continentality plays a major role in its climate. Yellowknife is situated approximately 565 km from the Arctic Ocean and 1210 km from the Pacific. The Rocky Mountains accentuate the great distance from the Pacific by impeding flow of maritime air toward the interior of the continent. Climatically, the study area is in the subarctic (Köppen and Geiger 1953). Precipitation and temperature regimes of the study area are represented by meteorological data for Yellowknife (15 km distant) covering the period 1941 to 1970 (Figure 3).

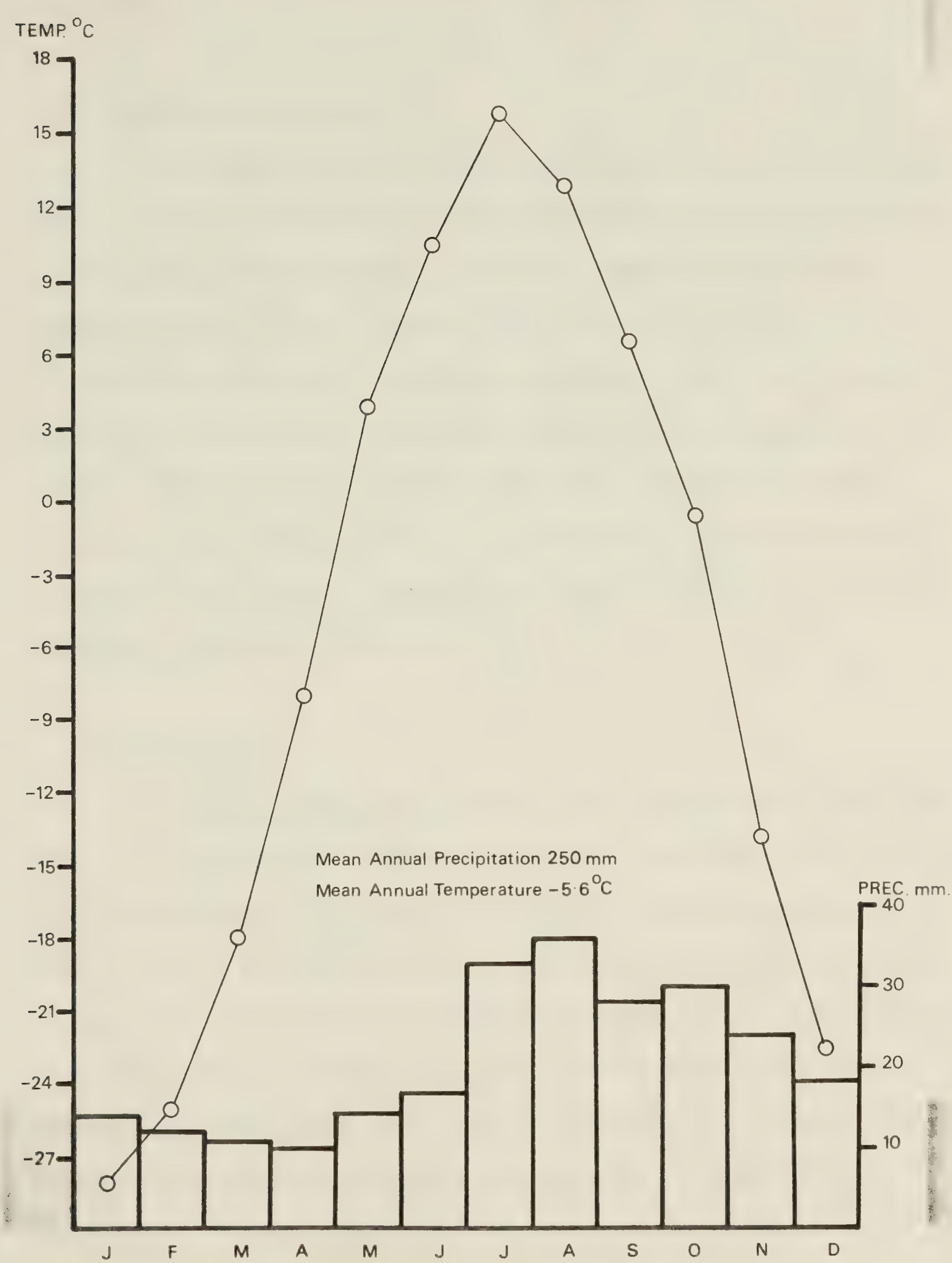
The continentality of the climate is shown by a large annual temperature range (Figure 3). Summers are cool, with July having a mean temperature of 15.6^{o}C. Winters are cold, having an average January temperature of -28.3^{o}C. Yellowknife's precipitation is moderately concentrated in late summer and early fall, and averages 250 mm annually (Figure 3).

1.4.2 STUDY AREA PHYSIOGRAPHY

Baker Creek Basin is situated on the Canadian Shield. Eighty-five per cent of the basin is underlain by Archaean granodiorite, granite and allied intrusive rocks (Wight 1973). The remaining 15 per-cent consists of the Yellowknife Greenstone Belt. Wight (1973) suggested that the region east of the basin was deglaciated 7000 years BP. Berry Hill which is the highest point in the basin is approximately 275 m above sea level. The lowest point in the basin is 167 m above sea level. Most aspects of relief are related to structure and lith-

Figure 3

Mean Monthly Temperature and Precipitation:
Yellowknife Northwest Territories



ology, although glaciation has imposed its characteristic surface morphology.

1.4.3 STUDY AREA VEGETATION

The study area lies in the open Boreal Woodland (Rowe 1959). Plant associations of the basin are divided into two major categories (Landals 1970), those occupying the upland ridge sites and those colonizing major valleys or depressions. The upland sites contain six distinct associations, while the depressions (the locations most important to the present study) are occupied by four separable associations. Dominant species of the study area depressions include: *Carex aquatilis, Betula pumila* var. *glandulifera, Ledum palustre* var. *decumbens, Picea mariana, Tomenthypnum nitens, Pohlia nutans, Cladonia coccifera,* and *Cladonia nivalis.*

1.5 FIELD SEASON

Field reconnaissance of Baker Creek Basin began 1 July 1973 when I was a research assistant to a Master's candidate in the Department of Geography, The University of Alberta. We used the Curtis (1959) transect sampling method to study vegetation in selected areas of the basin. That work was completed 31 August 1973. It was during that period that I selected the present area of study. The 1974 summer field season began on 1 June and extended to 31 August. Winter snow and temperature observations were made at the study site in March 1975. I spent a total of five months in the field.

1.6 CHOICE OF STUDY AREA

I chose the northeast sector of Baker Creek Basin (Figure 2) as the area of study for three reasons: the city of Yellowknife is relatively close to the study site, thus logistic support was reasonably available; the study location is situated northwest (generally upwind) of the mining operations of Yellowknife and far enough away (15 km) that air pollution from those operations has little or no environmental effect; and based on my familiarity with the location from having worked there during July and August 1973, I found the conditions well suited for this study.

CHAPTER TWO

VEGETATION

2.1 INTRODUCTION

Vast areas of Canada are covered by deposits of peat. Brown and Williams (1972) estimated that this type of terrain covers approximately 1,300,000 km^2. It extends from southern Canada northward to include parts of the continuous permafrost zone. This unique terrain is variously referred to as bogland, muskeg, organic terrain and peatland. The term peatland has many modern connotations, but for engineering purposes it is defined as *terrain composed of a living organic mat of mosses, sedges, and/or grasses, with or without tree growth, and underlain by a highly compressible mixture of partially decomposed and disintegrated organic material commonly known as peat* (MacFarlane 1959).

Organic terrain is composed of vegetal remains and its preserved state as peat reflects ordered processes (successional phenomena) which are a function of climatic, edaphic and biotic influences. Peatland can be classified by three methods: stratigraphically, geochemically and hydrotopographically.

Stratigraphically, peatlands rest directly on mineral ground or are underlain by limnic, organic sediments (Mörnsjö 1971). Peatland which is directly underlain by mineral ground indicates that the peat formed by paludification of the land. Peatland underlain by limnic,

organic sediments indicates that peat formation was initiated through the shoaling of a lake by an input of detritus. This process is called terrestrialization. Based on these broad stratigraphic characteristics, peatlands are genetically classed as paludificational peatlands or terrestrializational peatlands (Mörnsjö 1971).

The origin of water and concomitant nutrient supply is a primary factor differentiating peatland types. All peatlands receive water directly from precipitation; in some types of peatland, precipitation is the only source of moisture and consequently the primary source of mineral salts (Sjörs 1959). Such peatlands are ombrotrophic* and are sometimes called bogs. Geochemically, ombrotrophic peatlands have a pronounced deficiency in mineral nutrients, have highly acidic water and peat and low Ca/Mg ratios. Ombrotrophic peatlands are composed of peat types largely from *Sphagnum* spp. remains and physiognomically are of the domed type (Mörnsjö 1971).

Minerotrophic peatlands, or fens, receive varying amounts of water which have been in contact with mineral ground either as ground water or as surface runoff as well as precipitation. Geochemically, minerotrophic peatland has a high content of mineral nutrients and a higher Ca/Mg ratio than ombrotrophic peatland. Minerotrophic influence in peatlands usually results in a richer, more varied vegetation composed of species normally not present in ombrotrophic areas.

* Appendix 1 defines relevant terms

Hydrotopographically, ombrotrophic peatland is separated into three types; eccentrically domed bog peatland, concentrically domed bog peatland and forested bog peatland (Mörnsjö 1971). Eccentrically domed bog peatland is developed on gentle slopes of permeable ground in areas of high precipitation. From the top of its dome (located at the upslope margin) the peatland surface slopes downward as does the ombrogenous ground water level (Mörnsjö 1971). Developed in areas of flat terrain, concentrically domed bog peatland represents the classic raised bog with a centrally located dome. The ombrogenous ground water level slopes gently in all directions.

Ground water level in both the eccentrically and concentrically domed bog peatlands is high throughout the year. These peatlands are unwooded. Hydrologically the forest bog peatland is characterized by oscillations of ground water. From autumn to spring the ground water level is close to the peat surface. However, a pronounced water-deficit in summer favours the growth of trees. The surface of this peatland is only slightly domed, usually in a centrical manner.

Hydrotopographically, minerotrophic peatlands are classified into two separable types. The first type is termed rheo-geogenous, while the second is called topogenous (Mörnsjö 1971). Topogenous peatlands are separated into two subtypes termed topogenous-fens and topogenous-carrs. Rheo-geogenous minerotrophic peatlands are conditioned by laterally mobile ground water of continuous flow. These peatlands have a sloping surface and are usually found in areas of high precipi-

tation. Topogenous minerotrophic peatlands are developed in basins that contain stagnant ground water. These peatlands have a level surface. Topogenous fen peatlands maintain a high ground water level throughout the year. Topogenous carr peatlands are influenced by oscillating ground water levels. Primarily, the topogenous carr peatlands are composed of wooded peat whereas moss peat is the primary component of topogenous fen peatlands. It would seem (based on Mörnsjö's (1971) definitions) therefore, that the present work was conducted in a minerotrophic topogenous carr peatland.

Previous botanical research in the vicinity of the north arm of Great Slave Lake is limited (Landals 1970, Wight 1973). Early work (Richardson 1851, Macoun 1877, Preble 1908) was conducted along the margins of major waterways with the consequence that inland areas were unknown. With the advent of air travel that pattern changed. Raup (1946), Cody and Chillcott (1955), Scotter (1966) and Larsen (1971) conducted research proximal to the east arm of Great Slave Lake. Research south of the lake was executed by Harper (1931), Raup (1946) and Cody (1956). In the west, botanical investigations were made by Raup (1947), Cody (1960) and Theiret (1961).

With the exception of Raup's (1946) and Larsen's (1965, 1971) brief statements, no work is available for the Great Slave Lake area that analyzes plant succession in peatland areas. Therefore the present study is a contribution to the ecological knowledge of the Great Slave Lake area.

2.2 PROCEDURE

Phytosociologic methods as developed by Braun-Blanquet (1932) and modified by Gill (1971) are applied to the analysis of vegetation in the study area. The Braun-Blanquet method of community analysis is described as follows: a survey is made of a homogeneous plant community and all plant species present are recorded. Within the uniform area, preferably at a nodal position, a representative sample plot is established. If most of the listed species are not located in the sample plot it is enlarged until all or nearly all species are encountered. Once the minimum necessary plot size is established, floristic and environmental analyses are conducted.

The Braun-Blanquet method of community analysis is criticized (Janssen 1967) because the investigator selects homogeneous sample plots and does not take into consideration transitional vegetation between communities or associations. However, plant associations of the present study area have boundaries that are distinct with little ecotonation between them. Therefore, the Braun-Blanquet method of community analysis is an adequate study tool. Vegetation distribution in the study area was mapped from the ground with the aid of aerial photographs and from the air in a small aircraft.

2.2.1 SIZE OF SAMPLE PLOT

Sample plot size is selected to ensure that plot areas are sufficiently representative of each association. The problem in determining plot size is one of keeping it sufficiently small to handle while ensuring that it is large enough to contain representative

association information. In the present research area, the restricted distribution of some associations made it necessary for certain plots to be elongated. Plot sizes ranged from 4 m^2 in the smaller *Carex* associations to a maximum of 100 m^2 in the larger *Picea* stands. Twenty-four such plots are analyzed (six per association).

2.2.2 ANALYSIS OF SAMPLE PLOTS

After a tentative vegetation type is determined for an association, stratification of the component species in the sample plot is assigned as shown in Table 1.

TABLE 1 STRATIFICATION INDEX

A	Tree Layer	above 6 m
B	Low Tree/Tall Shrub Layer	below 6 m
C	Shrub-Herb Layer	below 1 m
D_1	Moss/Lichen Layer	on peat
D_2	Moss/Lichen Layer	on wood

A number (Table 2) denoting sociability is given to each species in the sample plot.

TABLE 2. SOCIABILITY INDEX

1	Growing singly
2	Grouped or tufted
3	Growing in small patches or cushions
4	Growing in extensive patches or carpets
5	Forming pure populations

A second number (Table 3) denoting average vigor of the species being evaluated is added.

TABLE 3. VIGOR INDEX

1	Dead
2	Dying
3	Poor
4	Good
5	Excellent

A figure from the cover-abundance index (Table 4) is given to each species.

TABLE 4. COVER-ABUNDANCE INDEX

x	Sparsely present, cover very small
1	Plentiful, covering 5 percent of area
2	Numerous, covering 6 - 25 percent of area
3	Covering 26 - 50 percent of area
4	Covering 51 - 75 percent of area
5	Covering more than 75 percent of area

Species importance in the study plot is assigned as shown in Table 5.

TABLE 5. SPECIES IMPORTANCE

1	0 - 19 percent of total plants
2	20 - 39 percent of total plants
3	40 - 59 percent of total plants
4	60 - 79 percent of total plants
5	80 - 100 percent of total plants

Using a Swedish increment borer, trees were aged by taking increment cores from five trees in each plot. Annual rings were counted by binocular microscope employing methods used by Parker (1971). The stems of *Salix* in some plots were cut and a direct growth-ring count was made in the field with the aid of a hand lens.

Once floristic analysis was complete, voucher specimens of each species of plant were collected from the sample plots. The specimens were processed and returned to The University of Alberta where final identification was made. Voucher specimens were deposited in the Herbarium of the Botany Department, The University of Alberta.

2.3 PLANT ASSOCIATIONS

Tables are often used to simplify the study of vegetation associations. The Associations Table (Table 6) depicts the cover abundance of species occuring in each study plot. Major inflection points are empirically seen between the *Carex* - *Tomenthypnum* and *Betula* - *Pohlia* associations. Comparison of active layer depths indicates relative homogeneity within each association but differences between them.

Tables 7 - 10 present separately, in tabular form, each association of the study area. The association tables denote the stratification, sociability, vigor, cover - abundance and importance values (Tables 1 - 5) for each species of a particular association. These indices are followed by their averages. Indicator species for each association are determined from those which have a high importance value and a high index of cover - abundance. Two indicator

TABLE 6

ASSOCIATIONS TABLE

ASSOCIATION	*Carex - Tomenthypnum*						*Betula - Pohlia*						*Ledum - Cladonia*						*Picea - Cladonia*					
PLOT NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
SPECIES																								
Tomenthypnum nitens	5	5	5	5	5	5			3	X														
Carex aquatilis	3	3	4	3	2	2	1	X	1	2	1	1												
Carex rostrata	3	3		2	3	1																		
Myrica gale			1	1	1	1	2	2	2	2	1	2												
Salix glauca		1	1		X				1	1	1	1												
Betula pumila var. *glandulifera*			X			1	2	2	2	1	2	2												
Potentilla palustris				X	1		X		1	X														
Eriophorum angustifolium					X					X														
Smilacina trifolia		X					1	X	X															
Pohlia nutans							5	5	2	5	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Chamaedaphne calyculata							2	2	2	1	1	1	2	2	1	2	2	3	X	X	1	1	1	1
Vaccinium uliginosum							1	1	2	1	2	1			X	X	X			X			X	
Picea mariana							X	X	X	X	1	X	1	1	X	X	X	X	5	5	5	5	5	5
Andromeda polifolia							X	X	X	X	X	X	1	1	1	1	1	1	1	1	1	1	X	1
Ledum groenlandicum							X	X	X	X	X	X	X	X	1	X	X	X	X	X	2	X	X	1
Potentilla fruticosa							X		X	1	1	1												
Rubus chamaemorus								X	1	X	X	X	1	1	1	1	1	1	1	1	1	1	1	1
Pinus banksiana									X	X	X	X												X
Cetraria pinstria							5				5		5						X	X	X	X	X	X
Campylium stellatum											5	2												
Ledum palustre var. *decumbens*							1		1				2	2	2	2	2	2	3	3	2	2	3	2
Salix pedicellaris								X	X															
Betula glandulosa							X																	
Larix laricina											X													
Oxycoccus microcarpus							X																	
Parnassia palustris var. *neogaea*												X												
Cladonia coccifera													3	3	3	3	3	3	X	X	1	X	X	X
Cladina mitis													1	1	1	2	1	1	2	3	2	2	2	3
Cladonia nivalis													1	1	X	2	1	1	3	2	3	3	3	2
Vaccinium vitis - idaea var. *decumbens*													1	X	1	1	X	X	1	1	1	1	1	1
Cladonia uncialis													1	X	1	X	X	X	X	1	X	1	X	X
Empetrum nigrum													1	X	X	1		1	1	1	X	1	1	1
Equisetum pratense													X				X				X			
Equisetum silvaticum													X				X			X	X			
Calamagrostis canadensis														X										X
Geocaulon lividum													X											
Hypogymnis physodes																			3	3	2	3	3	2

TABLE 7

Carex aquatilis - Tomenthypnum nitens Association

Plot Number		1				2				3				4				5				6				$\bar{x}$		
Stratum	Species	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Vigor	Cover - abundance	Importance
C	*Carex aquatilis*	2	5	3	3	2	5	2	3	2	5	4	4	2	5	4	3	2	4	2	2	2	5	3	2	4.8	3.0	2.8
	Carex rostrata	2	5	3	3	2	5	3	3					2	5	3	2	2	5	4	3	2	5	2	1	4.8	2.5	2.0
	Myrica gale									2	5	2	1	2	5	2	1	2	4	2	1	2	4	2	1	4.5	1.3	0.7
	Salix glauca					1	4	2	1	1	3	2	1					1	3	x	x					3.3	0.7	0.3
	Betula pumila var. *glandulifera*									2	4	x	x									2	4	2	1	4.0	0.3	0.2
	Potentilla palustris													1	5	x	x	1	5	1	1					5.0	0.2	0.2
	Eriophorum angustifolium																	2	4	1	x					4.0	0.2	x
	Smilacina trifolia					1	5	x	x																	5.0	x	x
D	*Tomenthypnum nitens*	3	4	2	5	3	4	3	5	3	4	2	5	3	4	2	5	3	4	2	5	3	4	3	5	4.0	2.3	5.0

TABLE 8

Betula pumila var. *glandulifer* - *Pohlia nutans* Association

Stratum	Species	7				8				9				10				11				12				X̄		
		Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Vigor	Cover - abundance	Importance
B	*Salix glauca*																	2	2	2	5					2.0	0.3	0.8
	Larix laricina																	1	4	X	X					4.0	X	X
C	*Betula pumila* var. *glandulifera*	2	5	4	2	2	5	3	2	2	5	3	2	2	4	2	1	2	5	3	2	2	5	3	2	4.8	3.0	1.8
	Myrica gale	2	5	3	2	2	5	3	2	2	5	3	2	2	5	3	2	2	5	3	1	2	4	3	2	4.8	3.0	1.8
	Chamaedaphne calyculata	2	5	3	2	2	5	3	2	2	5	2	2	2	5	2	1	2	4	2	1	2	5	2	1	4.8	2.3	1.5
	Vaccinium uliginosum	2	4	1	1	2	4	2	1	2	5	2	2	2	4	2	1	2	4	2	2	2	5	2	1	4.4	1.6	1.2
	Salix glauca									2	3	2	1	2	4	2	1	2	2	2	1	2	2	2	1	2.8	1.3	0.7
	Carex aquatilis	2	4	1	1	2	4	X	X	2	5	1	1	2	5	2	2	2	4	1	1	2	4	2	1	4.3	1.2	1.0
	Potentilla fruiticosa	1	4	X	X					1	5	X	X	1	5	1	1	1	5	1	1	1	5	2	1	4.8	0.7	0.5
	Ledum palustre var. *decumbens*	2	3	1	1					2	4	1	1													3.5	0.3	0.3
	Rubus chamaemorus					1	4	X	X	1	5	1	1	1	5	X	X	1	5	1	X	1	4	X	X	4.6	0.3	0.2
	Picea mariana	1	3	X	X	1	3	X	X	1	5	X	X	1	5	X	X	1	5	1	1	1	4	X	X	4.2	0.2	0.2
	Potentilla palustris	2	4	X	X					2	5	1	1	2	5	X	X									4.6	0.2	0.2
	Smilacina trifolia	1	4	1	1	1	4	X	X	1	5	X	X													4.3	0.2	0.2
	Andromeda polifolia	2	3	X	X	2	3	X	X	2	5	X	X	2	4	X	X	2	4	X	X	2	4	X	X	3.8	X	X
	Betula glandulosa	2	4	X	X																					4.0	X	X
	Eriophorum angustifolium													2	4	X	X									4.0	X	X
	Ledum groenlandicum	2	3	X	X	2	4	X	X	2	5	X	X	2	4	X	X	2	5	X	X	2	5	X	X	4.3	X	X
	Oxycoccus microcarpus	3	4	X	X																					4.0	X	X
	Parnassia palustris var. *neogaea*																					1	5	X	X	5.0	X	X
	Pinus banksiana									1	2	X	X	1	2	X	X	1	2	X	X	1	2	X	X	2.0	X	X
	Salix pedicellaris					2	3	X	X	2	4	X	X													3.5	X	X
D_1	*Pohlia nutans*	3	3	1	5	3	3	X	5	3	4	1	2	3	4	2	5	3	4	X	X	3	4	X	X	3.6	0.7	2.8
	Campylium stellatum																	3	4	1	5	3	4	2	2	4.0	0.5	1.2
	Tomenthypnum nitens									3	4	1	3	3	3	X	X									3.6	0.5	1.0
	Cetraria pinastria	3	4	X	5													3	4	1	5					4.0	0.2	1.7

TABLE 9

Ledum palustre var. *decumbens* - *Cladonia coccifera* Association

Plot number		13				14				15				16				17				18				$\bar{X}$		
Stratum	Species	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Sociability	Vigor	Cover - abundance	Importance	Vigor	Cover - abundance	Importance
C	*Ledum palustre* var. *decumbens*	2	5	3	2	2	5	3	2	2	4	3	2	2	4	3	2	2	4	3	2	2	5	3	2	4.5	3.0	2.0
	Chamaedaphne calyculata	2	5	3	2	2	5	3	2	2	4	2	1	2	5	3	2	2	5	3	2	2	5	3	3	4.8	2.8	2.0
	Andromeda polifolia	2	5	2	1	2	5	2	1	2	5	2	1	2	5	2	1	2	5	2	1	2	5	2	1	5.0	2.0	1.0
	Rubus chamaemorus	1	5	2	1	1	5	2	1	1	5	1	1	1	5	1	1	1	5	1	1	1	4	1	1	4.8	1.3	1.0
	Empetrum nigrum	3	4	2	1	3	5	1	X	3	4	X	X	3	4	2	1					3	4	2	1	4.2	1.2	0.5
	Ledum groenlandicum	2	4	1	X	2	5	X	X	2	4	2	1	2	4	2	X	2	4	2	X	2	5	X	X	4.3	1.2	0.2
	Vaccinium uitis - idaea var. *decumbens*	3	4	2	1	3	5	1	X	3	5	X	1	3	5	1	1	3	5	X	X	3	5	1	X	4.8	0.8	0.5
	Picea mariana	1	5	2	1	1	5	2	1	1	5	X	X	1	5	X	X	1	5	X	X	1	5	X	X	5.0	0.7	0.3
	Calamagrostis canadensis					1	3	X	X																	3.0	X	X
	Equisetum pratense	1	5	X	X													1	3	X	X					4.0	X	X
	Equisetum silvaticum	1	5	X	X													1	3	X	X					4.0	X	X
	Geocaulon lividum	1	4	X	X																					4.0	X	X
	Vaccinium uliginosum									2	3	X	X	2	3	X	X	2	3	X	X					3.0	X	X
D_1	*Cladonia coccifera*	4	5	4	3	4	5	3	3	3	5	4	3	4	5	3	3	3	5	3	3	3	5	1	3	5.0	3.0	3.0
	Cladina mitis	3	4	3	1	3	4	2	1	3	4	2	1	3	5	2	2	3	5	1	1	3	5	1	1	4.5	2.2	1.2
	Cladonia nivalis	3	4	2	1	3	4	2	1	3	4	X	X	3	5	2	2	3	5	1	1	3	5	1	1	4.5	1.3	1.0
	Cladonia uncialis	3	4	1	1	3	4	1	X	3	4	2	1	3	5	X	X	3	4	X	X	3	5	X	X	4.3	0.7	0.3
	Pohlia nutans	3	3	X	X	3	3	X	X	3	3	X	X	3	3	X	X	3	3	X	X	3	3	X	X	3.0	X	X
D_2	*Cetraria pinastria*	3	4	X	5																					4.0	X	0.8

TABLE 10

Stratum	Species	19 Sociability	19 Vigor	19 Cover - abundance	19 Importance	20 Sociability	20 Vigor	20 Cover - abundance	20 Importance	21 Sociability	21 Vigor	21 Cover - abundance	21 Importance	22 Sociability	22 Vigor	22 Cover - abundance	22 Importance	23 Sociability	23 Vigor	23 Cover - abundance	23 Importance	24 Sociability	24 Vigor	24 Cover - abundance	24 Importance	$\bar{X}$ Vigor	$\bar{X}$ Cover - abundance	$\bar{X}$ Importance
	Picea mariana - *Cladonia nivalis* Association																											
A	*Picea mariana*					1	4	X	5	1	3	X	5	1	4	2	5									3.7	0.3	5.0
B	*Picea mariana*	1	5	3	5	1	5	3	5	1	4	3	5	1	4	2	5	1	4	2	5	1	4	2	5	4.3	2.5	5.0
C	*Ledum palustre* var. *decumbens*	2	5	4	3	2	5	4	3	2	4	3	2	2	4	3	2	2	4	3	3	2	4	3	2	4.3	3.3	2.5
	Vaccinium vitis - idaea var. *decumbens*	3	5	2	1	3	4	1	1	3	5	2	1	3	5	2	1	3	5	1	1	3	5	2	1	4.8	1.7	1.0
	Empetrum nigrum	3	4	2	1	3	4	2	1	3	4	X	X	3	4	X	X	3	4	2	1	3	4	2	1	4.0	1.3	0.8
	Picea mariana	1	5	3	1	1	5	2	1	1	4	2	X	1	5	X	X	1	5	1	1	1	5	2	1	4.8	1.3	0.7
	Rubus chamaemorus	1	5	2	1	1	5	1	1	1	5	2	1	1	5	1	1	1	5	1	1	1	5	1	1	5.0	1.7	1.0
	Andromeda polifolia	2	5	2	1	2	5	2	1	2	5	1	1	2	5	1	1	2	5	X	X	2	5	2	1	5.0	1.7	0.8
	Chamaedaphne calyculata	2	3	X	X	2	3	X	X	2	4	2	1	2	4	1	1	2	4	2	1	2	4	2	1	3.7	1.2	0.7
	Ledum groenlandicum	2	5	X	X	2	4	1	X	2	5	3	2	2	4	X	X	2	4	X	X	2	4	2	1	4.3	1.0	0.5
	Equisetum pratense													1	5	1	X									5.0	0.2	X
	Equisetum silvaticum									1	5	X	X	1	5	1	X									5.0	0.2	X
	Calamagrostis canadensis																					2	3	X	X	3.0	X	X
	Pinus banksiana																					1	1	X	X	1.0	X	X
	Vaccinium uliginosum					2	2	X	X									2	2	X	X					2.0	X	X
D_1	*Cladonia nivalis*	4	5	4	3	4	5	3	2	4	5	4	3	4	5	4	3	4	5	4	3	4	5	3	2	5.0	3.7	2.7
	Cladina mitis	4	5	3	2	4	5	4	3	4	5	3	2	4	5	3	2	4	4	3	2	4	5	4	3	4.8	3.3	2.5
	Cladonia uncialis	3	4	X	X	3	5	2	1	3	4	X	X	3	5	2	1	3	4	X	X	3	3	X	X	4.2	0.7	0.3
	Cladonia coccifera	3	4	X	X	3	4	X	X	3	4	1	1	3	4	X	X	3	4	X	X	3	4	X	X	4.0	0.2	0.2
	Pohlia nutans	3	2	X	X	3	2	X	X	3	2	X	X	3	2	X	X	3	2	X	X	3	2	X	X	2.0	X	X
D_2	*Hypogymnia physodes*	3	4	1	3	3	5	1	3	3	5	1	2	3	4	1	3	3	4	1	3	3	5	1	2	4.5	1.0	2.7
	Cetraria pinastria	3	4	X	X	3	5	X	X	3	4	X	X	3	4	X	X	3	4	X	X	3	5	X	X	4.0	X	X

species, one from the A, B, or C stratum and one from the D stratum (Table 1) are chosen as nomenclature.

Thus the present research was conducted within four plant associations: the *Carex aquatilis* - *Tomenthypnum nitens*, *Betula pumila* var. *glandulifera* - *Pohlia nutans*, *Ledum palustre* var. *decumbens* - *Cladonia coccifera* and the *Picea* - *mariana* - *Cladonia nivalis*. Plants in each association (Tables 7 - 10) are ranked according to stratum and their average cover-abundance; where two or more plants have the same cover-abundance they are ranked according to their average species importance. If two species have identical importance and cover - abundance values they are ranked alphabetically.

2.4 PRESENT PLANT SUCCESSION

There is lack of agreement in the theoretical formulation of association interactions or of successional trends (Johnson and Valentine 1971). Braun-Blanquet (1932) stated that the exchange (appearance/disappearance) of species or of changes in the quantitative relations of species continuously present in vegetation associations constitutes the succession of one association to another. Drury and Nisbet (1973) explained that the term succession is usually used to imply sequences of time. They suggested that successional series are recognized as extending from associations of low stature, few species and simple structure to associations of tall plants, many species and complex structure. This concept is analogous to Braun-Blanquet's (1932) theory of pioneer, transitional and terminal stages of succession.

The *Carex* - *Tomenthypnum* association is the most simple in the present study area (Table 6). This association contains seven species in the richest sample plot. During spring and early summer, areas occupied by this association (Figures 4,5) are flooded to a shallow depth by snowmelt runoff. With the exception of permafrost lenses under hummocks, frozen material was absent from areas occupied by this association by 23 July (Figure 6, Appendix 2).

The *Betula* - *Pohlia* association occupies areas (Figures 4,5) characterized by individual peat hummocks. Eighteen species were found in the richest sample plot of this association. On 27 August no permafrost was found between the hummocks but average depth to frost beneath them was 64.0 ± .87 cm (Figure 6, Appendix 2).

Within the *Ledum* - *Cladonia* association a maximum of 17 species were found in any one sample plot. In areas occupied by this association (Figures 4,5) individual peat hummocks are no longer discernible. On 27 August permafrost was found beneath the peat surface of this association at a mean depth of 46.1 ± .75 cm (Figure 6, Appendix 2).

A maximum of 17 species were found in the richest sample plot of the *Picea* - *Cladonia* association. Permafrost was found beneath the peat surface at a mean depth of 45.8 ± 1.85 cm (Figure 6, Appendix 2).

2.5 SUMMARY

Four plant associations are present in depressions of the study area. Individually, the associations represent stages (pioneer, transitional and climax) of plant succession in a minerotrophic topogenous carr peatland.

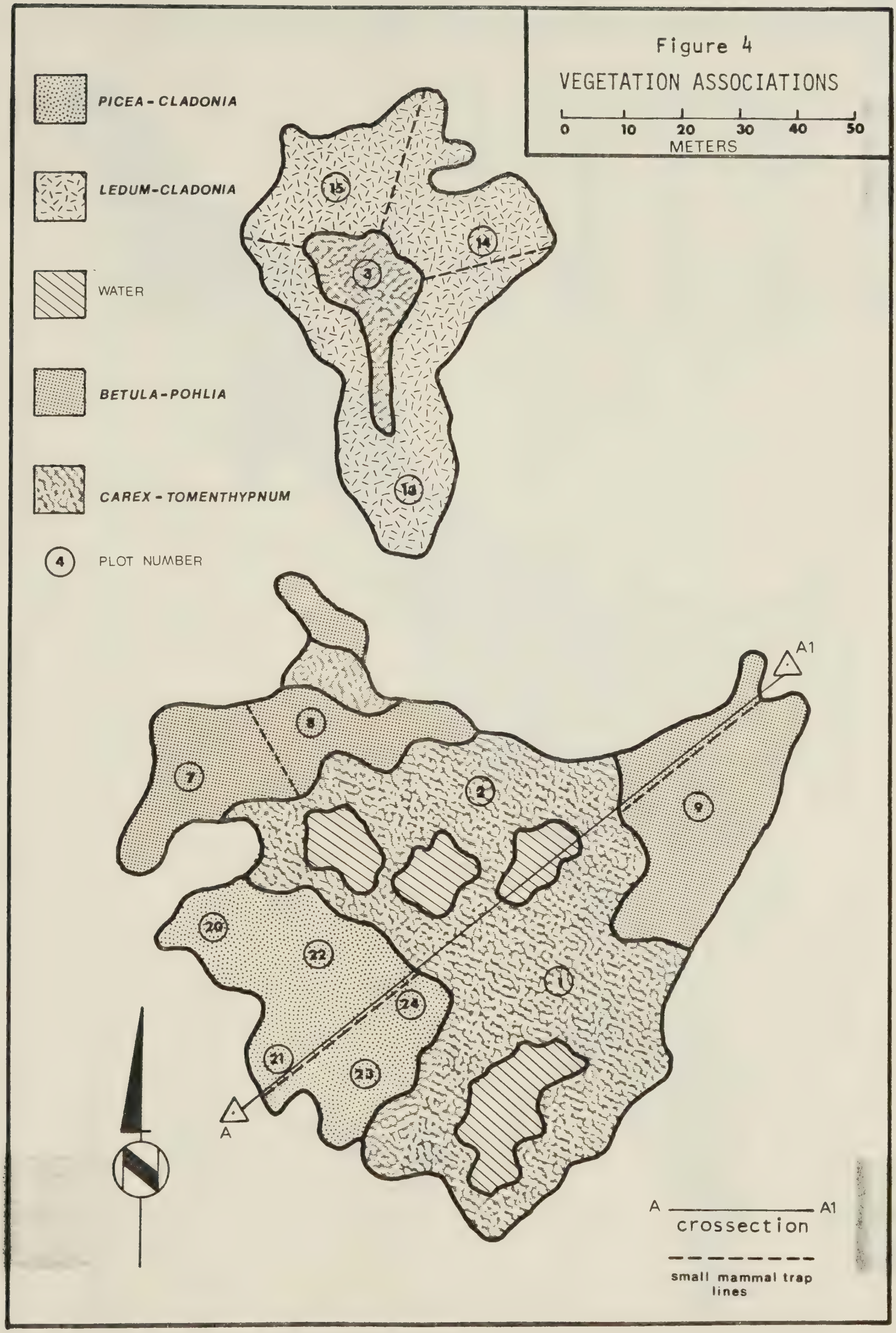


Figure 4
VEGETATION ASSOCIATIONS
0 10 20 30 40 50
METERS
PICEA - CLADONIA
LEDUM-CLADONIA
WATER
BETULA-POHLIA
CAREX - TOMENTHYPNUM
4 PLOT NUMBER
A1
A
A ——— A1
crossection
small mammal trap lines

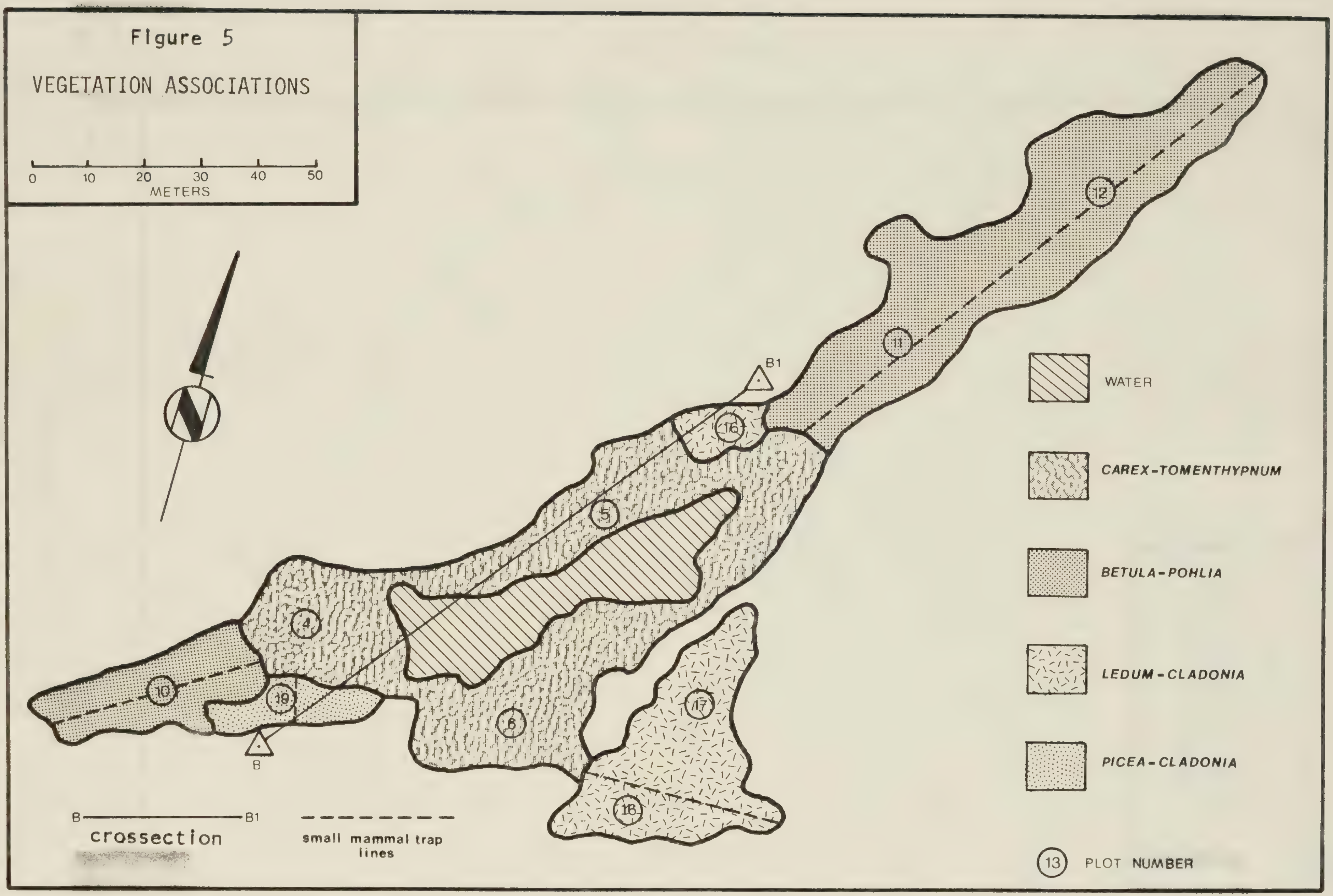
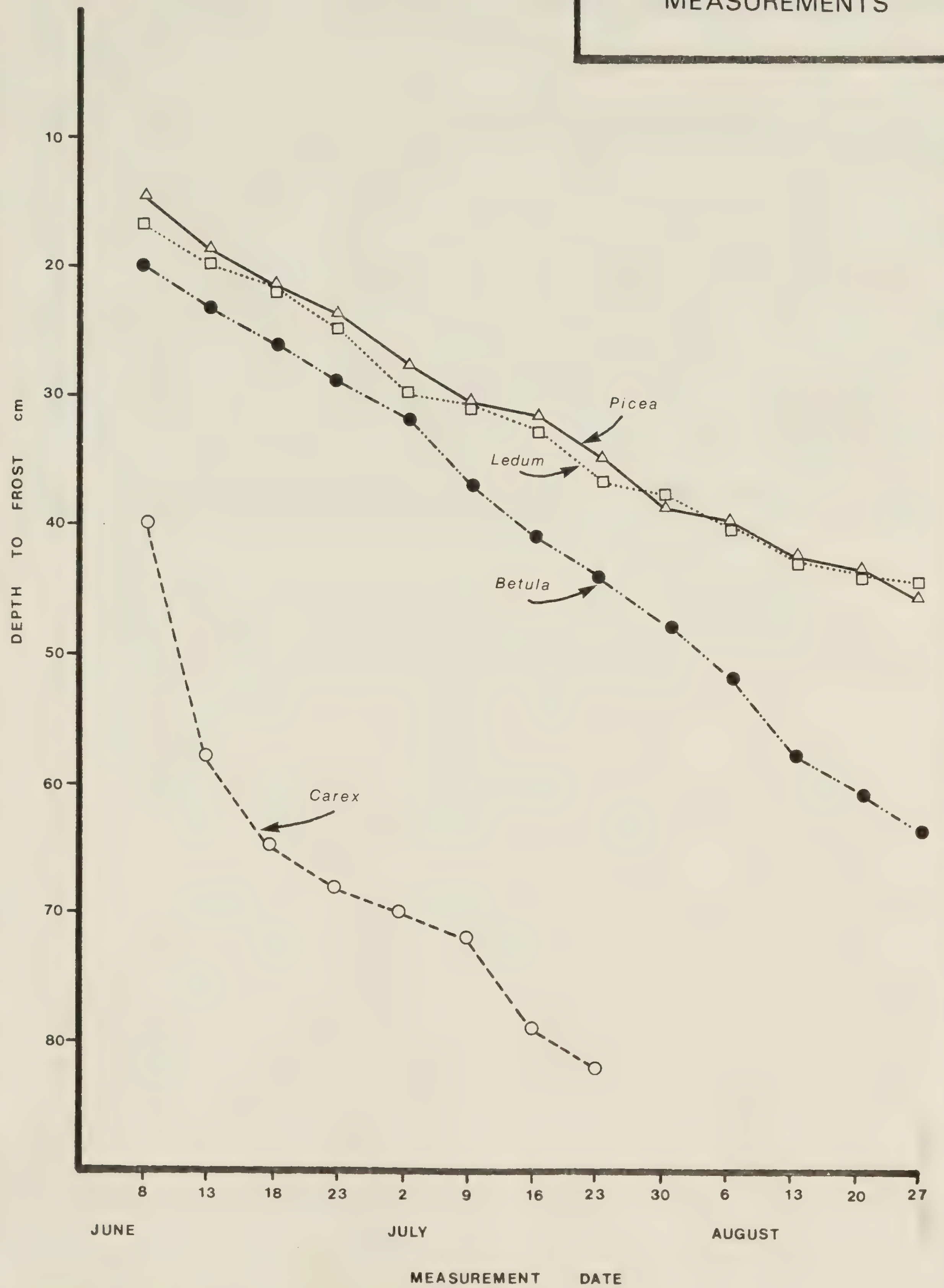


Figure 5

VEGETATION ASSOCIATIONS

Figure 6

DEPTH TO FROST MEASUREMENTS



The number of transition stages in sere development (a series of sequential stages which follow one another regularly) depends upon prevailing environmental conditions as well as upon the number of species important to the seral development (Braun-Blanquet 1932). Two transitional stages (represented by the *Betula* - *Pohlia* and the *Ledum* - *Cladonia* plant associations) are noted in the present study.

The *Picea* - *Cladonia* association represents the climatic climax stage of succession in the depressions of the study area. Braun-Blanquet (1932) stated that a climatic climax will not be reached at the same time over an entire area. The present study confirms this, as all stages of sere development occupy the depressions.

CHAPTER THREE

PALSA DEVELOPMENT

3.1 INTRODUCTION

Palsas are raised peat landforms with a permafrost core that commonly contains ice lenses no thicker than 2 - 3 cm (Lundqvist 1969). According to Lundqvist (1969) palsa uplift may be caused by the development of such ice lenses. Mackay (1965) described peat mounds domed by pressure from methane gas in the Mackenzie Delta area and suggested (Mackay 1972, personal communication in Washburn 1973) that such doming may initiate palsa development. Similar doming of peatland and ensuing palsa development in the Rock Lake Delta area of Alberta has been attributed to methane gas pressure (Gill, unpublished data, 1976). More commonly, however, the doming of peatland and subsequent palsa development is initiated by the volume expansion of water upon freezing (Lundqvist 1969).

There is controversy within the literature concerning whether the majority of palsa uplift occurs in mineral soil below organic material, or within the peat itself. Rapp and Rudberg (1964) stated that in northern Norway there have been many observations made of palsas both with and without a core of frozen mineral soil. In northern Sweden, Forsgren (1966) found that frozen mineral soil was only a small part of the total core of permafrost in most palsas. Ice lenses were more developed in the peat than in the mineral soil below and consequently most of the palsa height was ascribed to frost-heaving

within the peat. However, Fries (1964, in Forsgren 1968) found that peat thickness in palsas was the same as in the surrounding bogs and therefore attributed most of the organic material uplift to frost-heaving in mineral soil.

Salmi (1968) proposed that during their initial stages, palsas float on unfrozen saturated peat. He stated that after initiation, the permafrost core of a palsa is supplied with water from unfrozen saturated peat and mineral soil below the permafrost layer. At this stage of uplift, the volume of a palsa above the surrounding unfrozen organic material is similar to the ratio of ice above water to mass of ice below water in a floating iceberg. Zoltai (1972) stated that buoyancy alone does not account for the total elevation of a palsa above an unfrozen fen. In addition to buoyancy release, the volume of saturated peat increases, by about nine percent upon freezing, with most expansion taking place upward in the direction of heat loss. Therefore, it would seem that a combination of water migration to the freezing plane, buoyancy and water volume expansion upon freezing is needed to explain palsa uplift.

Salmi (1968) hypothesized that palsa uplift occurs when the permafrost layer within peat attains such a thickness that its lower surface comes in contact with mineral soil; at that point its upper surface begins to rise. Because of the ubiquitousness and greater thickness of ice lenses in fine grained mineral soil than in overlying peat, he claimed that mineral soil would undergo a greater volume change

than would the organic material. Research conducted by Zoltai and Tarnocai (1971) agreed with Salmi's (1968) explanation. They stated that in northern Manitoba mineral soil beneath peat was nearly level, except under areas that were frozen, at which point there was mineral soil uplift. The authors attributed doming of the peatland to this rise in the mineral soil substratum. It would seem therefore that to fully account for organic uplift by freezing, the best explanation involves a combination of the above processes.

3.2 PALSA AND PEAT PLATEAU DIFFERENTIATION

Zoltai (1972) suggested that permafrost in peat plateaux is entirely within the peat, but in palsas, although covered by peat, permafrost extends into underlying mineral soil. Peat plateaux therefore have frozen cores, and float on a saturated peat medium, whereas palsas are firmly anchored to mineral soil by their frozen cores. Zoltai (1972) also used differences in height to differentiate between palsas and peat plateaux. He stated that palsas vary in height between 100 cm and 300 cm but may reach 500 cm. Peat plateaux on the other hand seldom exceed 120 cm. He stated that freezing of mineral soil beneath peat gives the palsa increased height compared to the peat plateau.

Comparing Zoltai's (1972) definitions of palsas and peat plateaux to statements by Rapp and Rudberg (1964), Forsgren (1966) and Salmi (1968) which indicated that organic material uplift results from permafrost aggradation within peat, it appears that a peat plateau is a young palsa whose permafrost core has not reached mineral soil. Brown

(1968) has also stated that palsas and peat plateaux of subarctic Canada are morphological variations of the same process. Therefore a differentiation in formative processes between palsas and peat plateaux may not be needed, although a differentiation in the temporal attributes of the processes might be useful.

If a differentiation between palsas and peat plateaux must be made, it should be made on a more pertinent basis than Zoltai's (1972) classification. Such a distinction can be made using surface area. Sjörs (1961) stated that palsas are generally less than 100 m in diameter and peat plateaux are greater than 100 m. I feel that this criterion (if in fact needed) should be the basis on which to distinguish palsas from peat plateaux.

3.3 PALSA DEVELOPMENT

Zoltai's (1972) work shows that vegetation plays an important role in initiating palsa development. He stated that thin layers of permafrost develop under dense clumps of *Picea mariana* growing on a fen. Because the branches retain much of the winter snowfall as qali (Pruitt 1970), depths in the snow shadow beneath the trees (qaminiq) are thinner. This allows frost to penetrate deeper into organic material beneath the trees than in surrounding areas. In summer, shade from the same trees reduces solar radiation at the ground surface and retards thawing. The resultant negative heat balance over the years causes one to several thin layers of permafrost to develop, which may coalesce into larger layers (Zoltai 1972). Permafrost aggradation continues, together

with water migration along a thermal gradient (Hoekstra 1969), until the permafrost structure is at an environmental equilibrium (Zoltai 1972). Uplift of the frozen organic material takes place because of factors described previously. Due to uplift, surface peat is better drained and becomes drier, therefore its insulating effect is sufficient to reduce heat exchange above the permafrost during the summer.

Zoltai (1972) developed field criteria for the recognition of developmental stages of palsas. Without implying time periods, he used the terms *incipient, young, mature* and *overmature* to denote these changes. Although these stages of development were defined on a structural basis, the analysis was necessarily qualitative. He stated that the *incipient* palsa is aggrading and that the *mature palsa* is degrading. Zoltai stated that *young* palsas are usually less than 20 cm in height, whereas *mature* palsas are 100 cm or higher. He also defined palsas by their areal extent, stating that a *young* palsa is generally less than 200 m^2 while a *mature* palsa may reach several km^2.

Vegetation is a critical factor in Zoltai's (1972) description of the developmental stages of palsa formation. However, a less qualitative and clearer understanding of the stages of palsa development can be made by using vegetation in conjunction with palsa morphology, surface height above a water level datum, areal extent, active layer thickness and permafrost thickness.

3.4 PALSA DEVELOPMENT: MINEROTROPHIC TOPOGENOUS CARR PEATLAND

The present study develops field criteria to recognize developmental stages of minerotrophic topogenous carr palsas and to differentiate morphologically between these successive stages. The research is based on intensive field work conducted in three separate depressions in the study area. The depressions are occupied by small shoaling lakes surrounded by sedge meadows. During the spring snow-melt period, the meadows accumulate a shallow layer of water. By late summer, soil frost is virtually absent from the meadows except for lenses of permafrost that occur under hummocks. In some instances, contiguous to these meadows uplifted peatland contains a perennially frozen core.

3.4.1 PROCEDURE

The following procedures were used to determine the developmental stages of minerotrophic topogenous carr palsas.

1. Twelve transects were surveyed across the depressions of the study area.
2. The height of peat hummocks (having a perennially frozen core) above the sedge meadow water level datum (23 July) was determined by a survey rod and tape measure.
3. Weekly depth to soil frost measurements were made at nodal points within each plant association using a Hoffer probe.

4. An Abney level was used to determine the nodal point heights of the *Ledum* - *Cladonia* and *Picea* - *Cladonia* plant associations above the water level datum of the sedge meadow. However, as the height differences were minimal, I found that the instrument did not provide sufficiently accurate measurements.
5. Snow depth measurements were made during March, 1975 at nodal points within each plant association using a meter stick.

3.4.2 HUMMOCKS

Depressions of the study area are occupied by small shoaling lakes surrounded by sedge meadows of the *Carex* - *Tomenthypnum* plant association (Figures 4, 5, 7, 8). During spring and early summer the meadows are flooded to a shallow depth by snowmelt runoff. During particularly wet years, as was the case in 1974, sedge meadows may be flooded all summer. In 1974, seasonal soil frost thawed rapidly because water (acting as a heat source) remained on the meadow, and underlying peat remained saturated allowing rapid conductive heat transfer. Buckman and Brady (1969) estimated that heat passes from water to soil 150 times more rapidly than from air to soil.

With the exception of permafrost lenses under scattered hummocks, soil frost was absent from the *Carex* - *Tomenthypnum* meadows by 23 July (Figure 6, Appendix 2). These hummocks varied from 14 to 35 cm in height above the 23 July water level datum of the meadow and had an

Figure 7

IDEALIZED CROSSECTION

$A - A_1$

Location reference: Figure 4

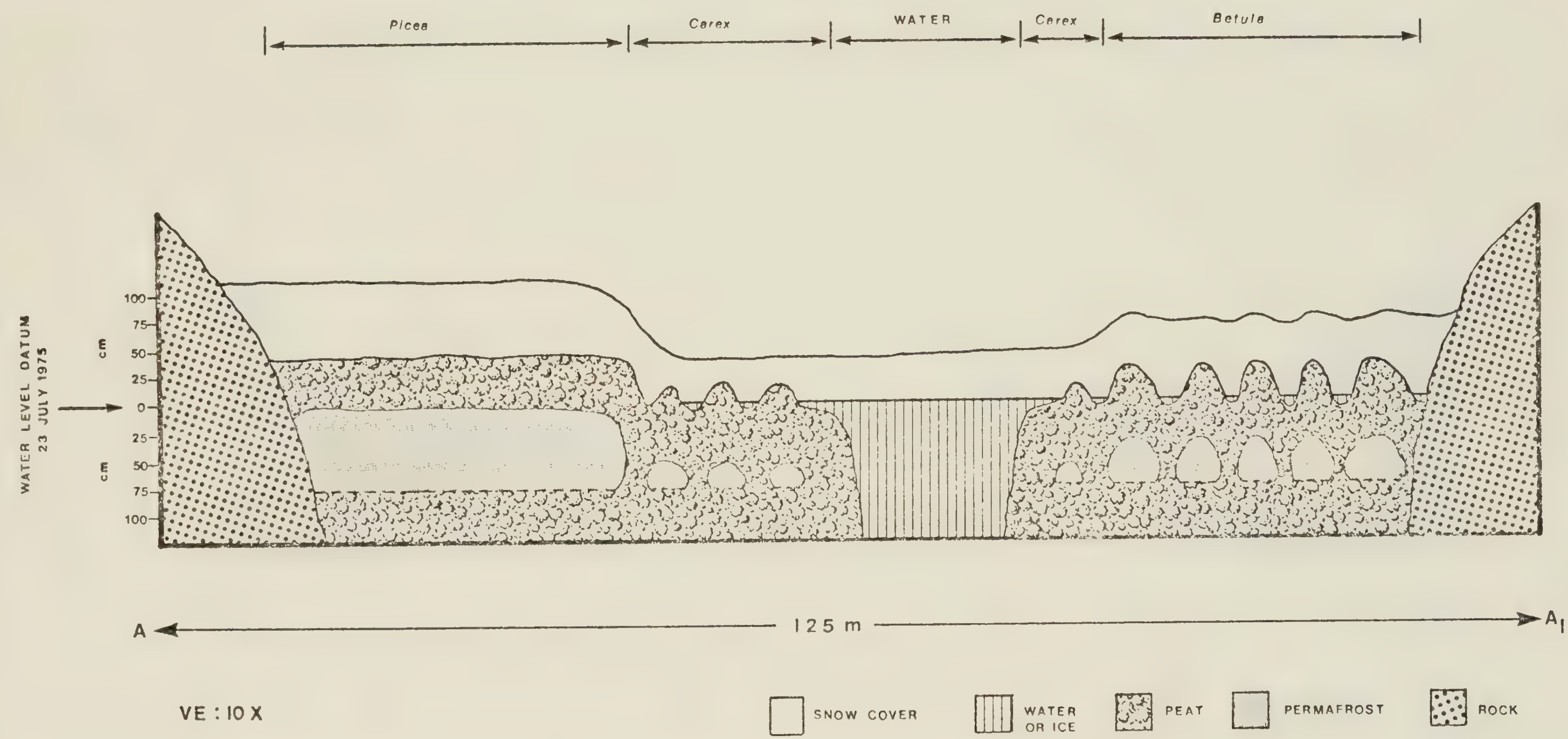
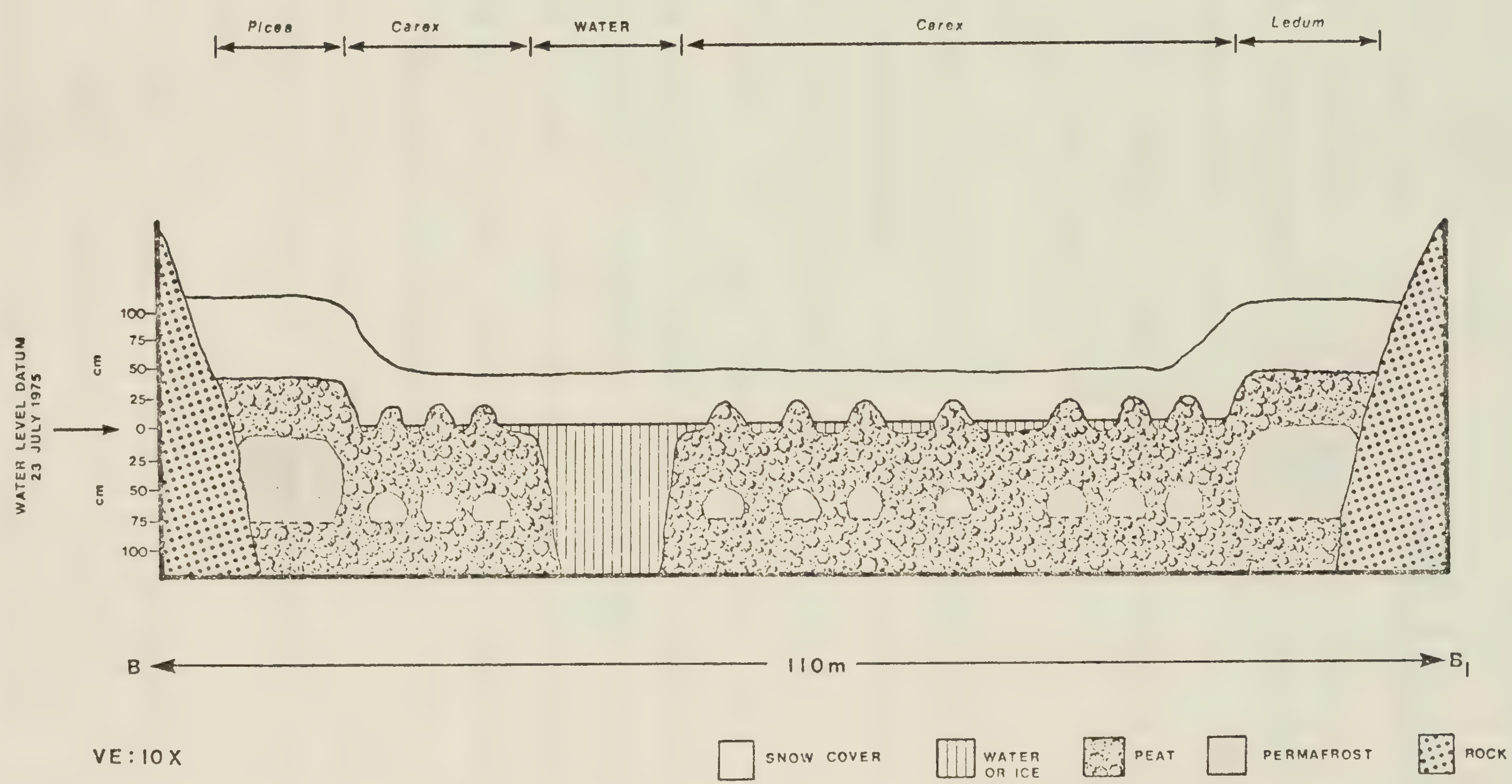


Figure 8

IDEALIZED CROSSECTION

$B - B_1$

Location reference: Figure 5



average relief of 24.2 ± 1.5 cm (Appendix 3). Mean active layer depth within the hummocks was 68 cm on 27 August.

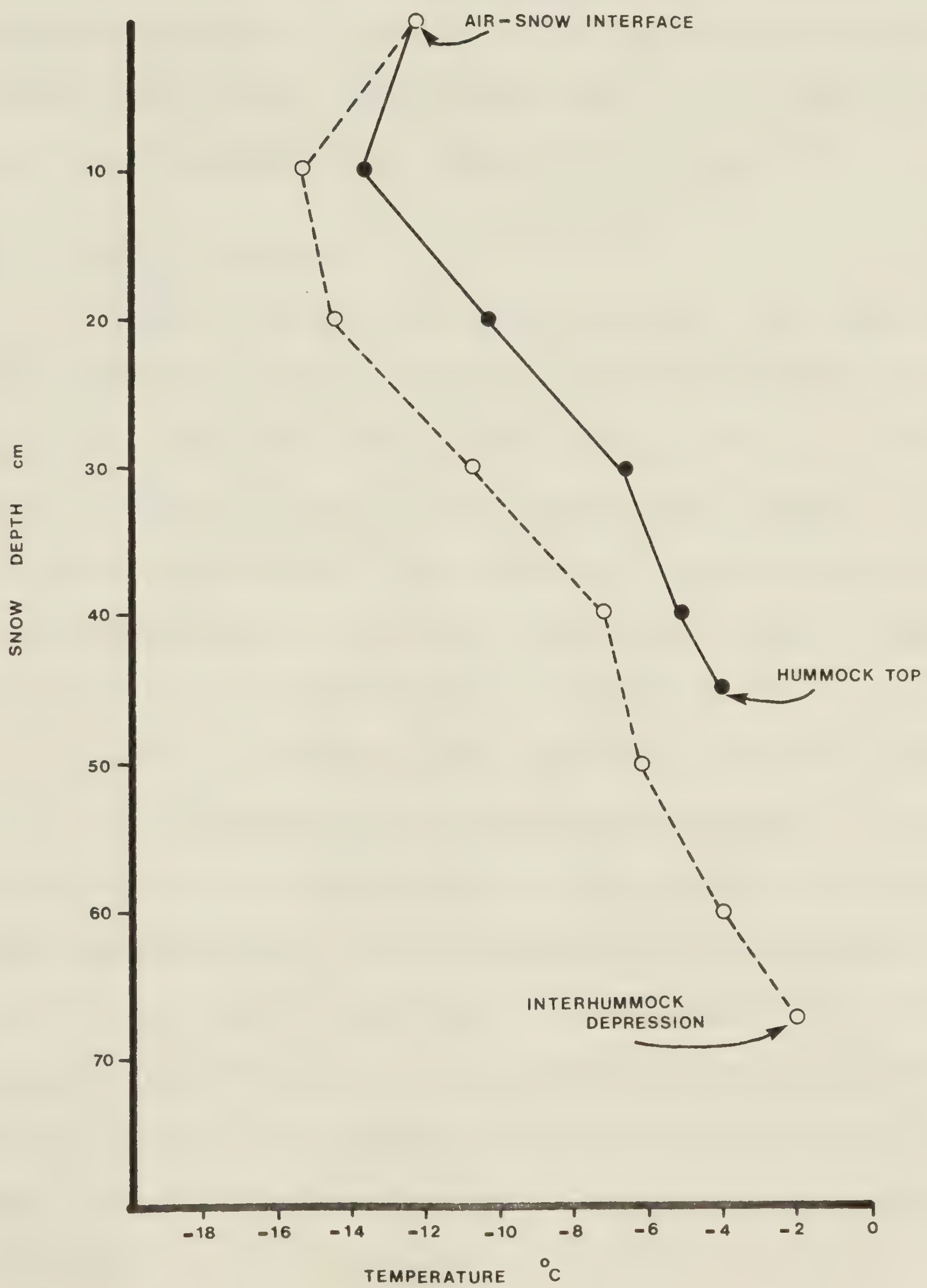
Continguous to the *Carex* - *Tomenthypnum* hummocks are other hummock areas dominated by the *Betula* - *Pohlia* association (Figures 4, 5, 7). These hummocks varied from 27 to 43 cm in height above the 23 July water level datum and had a mean relief of 34.5 ± 1.0 cm (Appendix 3). On 27 August frost was absent between the hummocks. However, average active layer depth within the hummocks was 64.0 ± .87 cm (Figures 6, Appendix 2).

The development of permafrost lenses in certain areas of sedge meadows but not in others appears to be caused by the following conditions. Fall rains, which are followed by low snowfalls in early winter, are important factors. Fall rain causes sedge tussocks and peat hummocks to become wet, which facilitates heat transfer (Buckman and Brady 1969) to the surface by conduction. Freezing temperatures cause further heat loss from the tussocks and hummocks, particularly if there is little snow to retard heat transfer. As snow accumulates during early winter, inter-hummock depressions fill before the hummocks are covered. The thermal resistance created by early and deeper snow between hummocks acts as an effective localized insulating layer against frost penetration.

By March 1975, snow depth was approximately 22 cm deeper between hummocks of the *Betula* - *Pohlia* plant association than on the hummock crests (Figure 9, Appendix 4). Concomitantly, the hummock snow-peat interface temperature was approximately 2^{o}C colder than the snow-peat interface temperature of the inter-hummock depression (Figure 9).

Figure 9

SNOW DEPTH AND TEMPERATURE



Although similar measurements were not made on hummocks of the *Carex* - *Tomenthypnum* association, I assume that the greater snow depth between those hummocks also acted as a localized thermal resistance to heat loss. During the summer, uplifted hummock peat is better drained and becomes drier than meadow peat, therefore its insulating effect is sufficient to reduce heat exchange above the permafrost. As a result, permafrost lenses that form beneath the hummocks are preserved.

3.4.3 UPLIFTED PEATLAND

Proximal to the hummocks of the *Carex* - *Tomenthypnum* and *Betula* - *Pohlia* plant associations are areas of undulating peatland having a perennially frozen core. These palsas are occupied by the *Ledum* - *Cladonia* and *Picea* - *Cladonia* plant associations (Figures 4, 5, 7, 8). On 23 July, the surface of these palsas was approximately 45 cm above the sedge meadow water level datum. Mean active layer thickness was 46.1 $\pm$ .75 cm on 27 August (Figure 6, Appendix 2).

Palsa development results from slow peat infilling of depressions as well as permafrost aggradation between hummocks. During summer in the *Ledum* - *Cladonia* association, the high albedo of *Cladonia* spp. lichen coupled with the insulating effect of dry uplifted peat is sufficient to reduce heat exchange above the permafrost. Within the *Picea* - *Cladonia* association, trees displace the energy exchange surface upward from the air-peat interface and further reduce heat exchange above permafrost. Therefore, an increasing amount of peat remains frozen throughout the summer.

3.4.4 THERMOKARST FEATURES

Shallow, water-filled thermokarst depressions are present on some palsas occupied by the *Picea - Cladonia* plant association. Active layer thickness beneath one thermokarst pool was 54 cm on 27 August. It appears that these features are initiated when water collects in shallow depressions during periods of high precipitation. The organic material beneath them thus remains saturated, which facilitates heat transfer (Buckman and Brady 1969) by conduction, resulting in thawing of the permafrost.

3.5 SUMMARY

Palsa uplift (development of permafrost) is principally caused by water migration to the freezing plane, volume expansion of water upon freezing (Rapp and Rudberg 1964, Forsgren 1966, Salmi 1968, Lundqvist 1969, Zoltai 1972) and by the buoyancy effect created by frozen organic material overlying saturated unfrozen peat (Salmi 1968, Zoltai 1972). In some peatlands, permafrost and accompanying palsa development is initiated under dense clumps of *Picea mariana* (Zoltai 1972). The present research indicates that in minerotrophic topogenous carr peatland, permafrost genesis and palsa initiation occurs in sedge meadows occupied by the *Carex - Tomenthypnum* plant association. Over time, slow peat infilling of depressions between permafrost hummocks as well as permafrost aggradation creates an uplifted peatland having a perennially frozen core. These palsas are then occupied by the *Ledum - Cladonia* and *Picea - Cladonia* plant associations.

CHAPTER FOUR

SMALL MAMMALS

4.1 INTRODUCTION

Most small mammal research near Great Slave Lake has been centered at the Heart Lake Research Station of The University of Alberta. Similar research in the vicinity of the north arm of Great Slave Lake is limited. As well, no previous work is available that studies the suitability of minerotrophic topogenous carr peatland as small mammal habitat or determines which particular plant associations of this peatland contain the most number of small mammal species.

4.2 PROCEDURE

To understand the interrelations of small mammals and differing palsa habitats the following procedures were used.

1. Eleven snap trap lines were set across the three depressions of the study area. Each line extended 20 m onto bedrock adjacent to the peatland.
2. Trapping stations were spaced at 5 m intervals along the lines. Two traps (baited with peanut butter) were placed at each station.
3. Each line was left in position for two 20-day periods (24 June - 14 July, 1 August - 21 August) and checked daily.

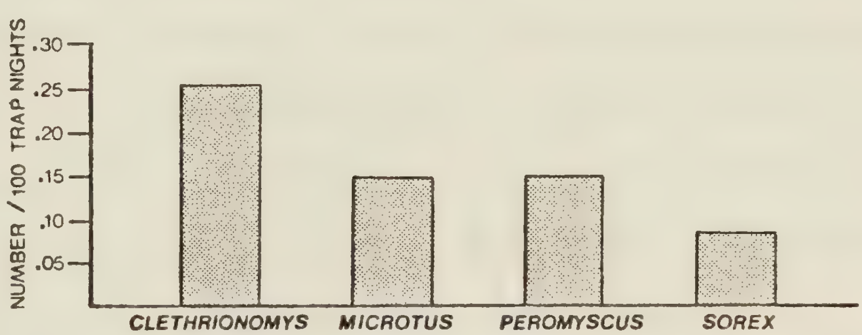
4. Each trapped animal was weighed and length measurements were made of the right hind foot, right ear, tail and body. Skulls of the animals were processed and returned to The University of Alberta where final identification was made by Dr. W. A. Fuller, Department of Zoology.

4.3 SPECIES DISTRIBUTION

One species of shrew *(Sorex cinereus)* and three rodents of the Family Muridae *(Clethrionomys rutilus, Peromyscus maniculatus* and *Microtus pennsylvanicus)* were trapped in the study area. By combining data from both trapping periods and from all habitats, the relative abundance of each species was calculated (Figure 10).

Figure 10

RELATIVE SPECIES ABUNDANCE

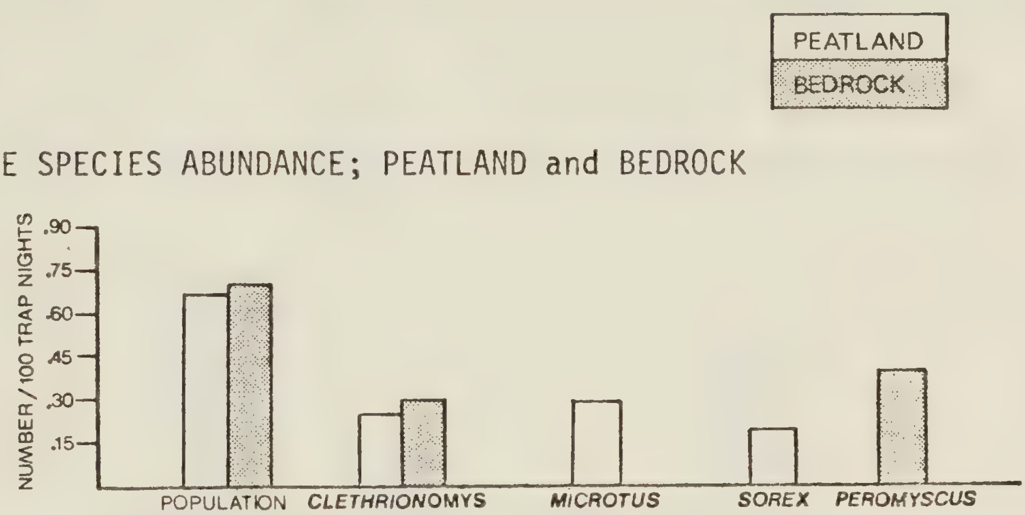


Clethrionomys rutilus is clearly the most numerous small mammal (40 percent of catch) of the study area. *Microtus pennsylvanicus* and *Peromyscus maniculatus* are equally present and comprise approximately 23 percent of the catch. *Sorex cinereus* represents 14 percent of the catch.

Figure 11 compares the total population and the abundance of each species trapped on the peatland to that of bedrock. Although somewhat higher on bedrock (.68 animals per 100 trap nights), species richness is not significantly greater than peatland (.64 animals per 100 trap nights).

Figure 11

RELATIVE SPECIES ABUNDANCE; PEATLAND and BEDROCK



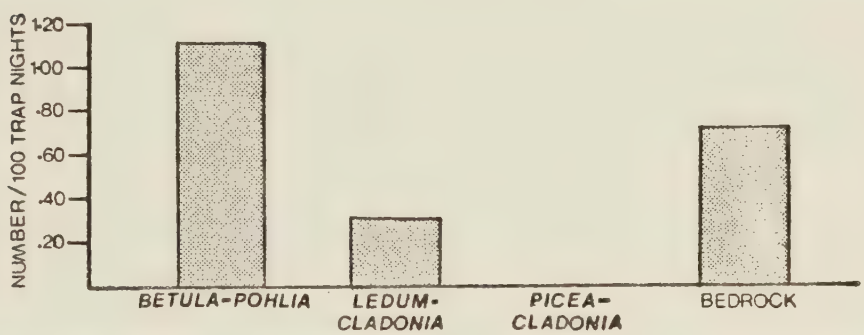
Clethrionomys rutilus has a relatively even distribution in bedrock and peatland habitats. However, the other three species are much more restricted in habitat range. *Microtus pennsylvanicus* and *Sorex cinereus* were exclusively trapped in peatland habitats, whereas *Peromyscus maniculatus* was trapped only in bedrock habitats. As shown by Banfield (1974), *Peromyscus maniculatus* seldom selects wet habitats, whereas *Microtus pennsylvanicus* prefers such areas.

Within the peatland, species abundance is greatest in the *Betula* - *Pohlia* plant association (Figure 12). Due to a continuous water cover throughout the summer, trapping of small mammals was not conducted in the *Carex* - *Tomenthypnum* plant association. However,

research indicates that at each stage of succession toward the climax *Picea - Cladonia* plant association, species abundance decreases. The reasons for this are unknown, but they may be attributed to the increase of *Ledum palustre* var. *decumbens* (Fuller, personal communication, 1976). *Ledum palustre* var. *decumbens* contains ledol, a poisonous substance causing cramps and paralysis in humans (Hulten 1968), which may also have an adverse effect on small mammals.

Figure 12

RELATIVE SPECIES ABUNDANCE; PLANT ASSOCIATIONS and BEDROCK



4.4 SPECIES DIVERSITY

Species diversity of the *Betula - Pohlia*, *Ledum - Cladonia* and *Picea - Cladonia* plant associations, as well as the bedrock habitat is calculated using Brillouin's formula (Pielou 1966, Table 11, Appendix 5). Eveness of the plant associations was determined using Pielou's (1966) formula (Table 11).

TABLE 11: SPECIES DIVERSITY AND EVENNESS

	Species Diversity	Evenness
Habitat 1 *Betula - Pohlia*	.46	.76
Habitat 2 *Ledum - Cladonia*	.45	.75
Habitat 3 *Picea - Cladonia*	0	0
Habitat 4 Bedrock	.29	.49

4.5 SUMMARY

Four species of small mammals (*Sorex cinereus, Clethrionomys rutilus, Peromyscus maniculatus* and *Microtus pennsylvanicus*) were trapped in the study area. Equally present in the bedrock and peatland habitat, *Clethrionomys rutilus* represents 40 percent of the catch. However, *Microtus pennsylvanicus, Peromyscus maniculatus* and *Sorex cinereus* are much more restricted in habitat range. At each stage of succession toward the climatic climax, species abundance, diversity and evenness decreases.

CHAPTER FIVE

CONCLUSIONS

5.1 INTRODUCTION

This research describes the sequence of environmental conditions that contribute to the development of minerotrophic topogenous carr peatland ecosystems near Yellowknife, Northwest Territories. The study indicates that permafrost aggradation in organic terrain contributes to the development of distinct physical environments within which characteristic plant associations evolve. Concurrently, differing plant associations provide habitats of varying suitability for small mammals. Although the natural environment does not function in compartments (either in time or space), sectioning is valuable in some instances in reconstructing environmental time sequences (Gill 1972). Therefore, I hypothesize that three stages represent the interaction between minerotrophic topogenous carr palsa development and the formation of small mammal habitat.

5.2 STAGE ONE

Minerotrophic topogenous carr palsa formation initially takes place in *Carex* - *Tomenthypnum* meadows where individual peat hummocks develop a perennially frozen core. Snowmelt runoff floods the meadows to a shallow depth during spring and early summer. During particularly wet summers *Carex* - *Tomenthypnum* meadows may be flooded continuously.

With the exception of permafrost lenses under hummocks, seasonal soil frost is usually absent from the sedge meadows by August.

Although small mammal trapping was not conducted in the *Carex* - *Tomenthypnum* meadows of the present research area, I assume that this plant association has low suitability as small mammal habitat because of its wetness. In particular, *Peromyscus maniculatus* seldom occurs in wet habitats, *Clethrionomys rutilus* prefers areas covered by shrubby growths of willow and birch, and *Sorex cinereus* inhabits moist shrubby areas with a duff ground cover (Banfield 1974).

5.3 STAGE TWO

Over the years, organic accretion and permafrost aggradation cause the individual peat hummocks of the *Carex* - *Tomenthypnum* meadows to become larger and more numerous. The surface of these larger hummocks is drier than that of the *Carex* - *Tomenthypnum* hummocks, enabling the *Betula* - *Pohlia* plant association to become dominant.

Small mammal trapping indicates that species abundance is greatest in the *Betula* - *Pohlia* plant association. Therefore, I assume that areas dominated by this association provide the most suitable small mammal habitat of the peatland.

5.4 STAGE THREE

Slow peat infilling of depressions between hummocks as well as permafrost aggradation results in an uplifted palsa having a perennially frozen core. The uplifted palsa surface is drier than

the peat surface of the *Betula - Pohlia* hummocks which results in the dominance of the *Ledum - Cladonia* plant association. Over the years, sere development continues and the *Ledum - Cladonia* plant association is replaced by the *Picea - Cladonia* association.

Small mammal trapping indicates that species abundance in the *Ledum - Cladonia* associaton is less than in the *Betula - Pohlia* association but higher than in the *Picea -Cladonia* association. Consequently, I assume that the habitat suitability of minerotrophic topogenous carr peatlands is greatest in the *Betula - Pohlia* plan association and decreases toward the climatic climax *Picea - Cladonia* association.

5.5 SUMMARY

Peatland of the present research area is occupied by four separate plant associations. Each plant association possesses a discrete set of environmental conditions which are reflected by three stages of succession to a climatic climax. The differing plant associations provide habitats of varying suitability for small mammals.

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APPENDIX 1

Relevent Terms

For purposes of the present research, the following definitions are adhered to (Mörnsjö 1971; Whittaker 1975):

OMBROTROPHIC	Communities that receive nutrients from the atmosphere.
MINEROTROPHIC	Communities that receive nutrients from both the atmosphere and mineral soil.
TOPOGENOUS	Minerotrophic peatlands that develop in basins containing stagnant ground water.
CARR	Topogenous peatlands that are influenced by oscillating ground water levels.

APPENDIX 2

Depth To Frost Measurements

PLANT ASSOCIATION	DATE	DEPTH IN CM										$\bar{X}$	SE
	8 June	39	41	40	40	41	41	40	41	40	40	40.3	.21
	13 June	59	60	57	58	58	59	57	58	58	57	58.1	.31
	18 June	65	66	67	65	66	67	64	65	66	67	65.8	.33
	23 June	69	70	69	69	68	70	69	69	68	68	68.9	.23
Carex - Tomenthypnum	2 July	70	71	70	70	69	71	70	70	69	70	70.0	.21
	9 July	72	73	73	73	72	73	72	73	71	73	72.5	.22
	16 July	78	79	80	81	82	79	78	80	79	81	79.7	.42
	23 July	82	84	--	--	--	81	82	--	--	--	82.3	.63
	30 July	No Frost											
	8 June	19	21	19	20	18	21	22	20	23	23	20.6	.54
	13 June	21	23	22	22	20	23	25	22	26	27	23.1	.71
	18 June	24	26	25	25	22	27	28	26	28	29	26.0	.67
	23 June	27	28	27	28	26	31	31	30	31	31	29.0	.63
	2 July	30	31	30	30	29	35	34	35	38	35	32.7	.97
	9 July	32	36	35	35	32	40	39	41	42	41	37.3	1.19
Betula - Pòhlia	16 July	35	39	40	40	35	45	43	44	47	45	41.3	1.33
	23 July	40	40	45	41	40	47	48	46	50	48	44.5	1.23
	30 July	44	43	46	44	45	49	51	53	55	50	48.0	1.33
	6 August	50	48	52	49	47	55	56	54	60	55	52.6	1.30
	13 August	52	54	60	55	50	61	62	60	66	62	58.2	3.40
	20 August	59	60	62	61	58	65	63	61	66	64	61.9	.82
	27 August	63	62	64	62	60	67	65	62	69	66	64.0	.87

PLANT ASSOCIATION	DATE	DEPTH IN CM										$\bar{X}$	SE
Ledum - Cladonia	8 June	15	14	14	15	16	16	17	15	18	15	15.5	.40
	13 June	19	18	20	18	18	19	20	19	20	20	19.1	.28
	18 June	20	23	24	22	23	24	22	23	22	24	22.7	.40
	23 June	21	25	26	23	26	29	26	28	24	29	25.7	.82
	2 July	25	29	30	30	30	34	30	30	29	34	30.1	.81
	9 July	27	30	30	31	31	35	32	33	32	34	31.5	.72
	16 July	30	31	30	32	34	35	37	34	38	34	33.5	.87
	23 July	31	37	34	37	38	39	39	37	43	36	37.1	1.01
	30 July	35	41	38	38	39	41	39	38	43	39	38.9	.72
	6 August	36	41	40	38	41	44	40	42	45	40	40.7	.83
	13 August	41	45	42	40	44	46	42	42	40	42	43.4	.93
	20 August	43	45	45	43	44	46	43	45	50	43	44.7	.68
	27 August	43	46	45	44	46	47	45	59	51	45	46.1	.75
Picea - Cladonia	8 June	19	18	19	18	19	18	16	15	16	15	17.3	.51
	13 June	23	21	20	21	23	19	17	19	17	20	20.0	.66
	18 June	30	26	25	25	24	20	18	20	19	22	22.9	1.19
	23 June	32	30	26	26	25	21	19	22	21	23	24.5	1.31
	2 July	34	33	29	29	28	27	24	28	25	28	28.5	.98
	9 July	38	35	32	34	30	30	25	30	28	30	31.2	1.17
	16 July	40	39	33	35	33	30	26	30	29	33	32.8	1.38
	23 July	41	40	40	40	36	32	29	32	31	35	35.6	1.41
	30 July	42	47	44	49	39	33	32	36	32	36	39.0	1.97
	6 August	43	47	44	49	42	35	34	36	34	30	40.4	1.73
	13 August	48	50	47	50	46	36	35	41	34	43	43.0	1.96
	20 August	50	51	47	50	47	38	37	41	36	44	44.1	1.82
	27 August	51	53	49	51	50	39	39	44	37	45	45.8	1.85

APPENDIX 3

Hummock Heights Above Water Level
Datum 23 July 1975

PLANT ASSOCIATION	HUMMOCK HEIGHTS (cm)										$\bar{x}$	se.
Carex - Tomenthypnum	20	16	18	19	27	29	25	32	30	26	24.15	1.46
	21	17	19	29	33	26	16	31	35	14		
Betula - Pohlia	28	31	29	27	32	40	43	36	37	41	34.50	1.04
	29	32	34	35	40	39	31	36	37	33		

APPENDIX 4

Snow Depth Measurements
25 March 1975

NODAL POSITION	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	$\bar{x}$	se.
ASSOCIATION	SNOW DEPTH (cm)																					
Picea - *Cladonia* (api)	77	77	75	68	77	78	64	71	66	51	80	63	63	75	70	65	81	70	66	68	70.3	1.66
Picea - *Cladonia* (qamaniq)	62	64	63	52	52	61	56	57	67	51	57	60	63	59	60	65	57	63	65	60	59.7	1.02
Ledum - *Cladonia*	70	58	66	56	64	59	64	58	55	54	63	70	50	71	68	69	72	70	64	69	63.5	1.47
Betula - *Pohlia* (hummocks)	46	47	48	48	48	49	46	48	42	40	41	48	46	48	46	46	48	40	45	41	45.6	.68
Betula - *Pohlia* (interhummock depressions)	66	63	66	67	68	70	67	71	70	72	68	64	69	63	71	66	68	67	70	70	67.8	.59
Carex - *Tomenthypnum*	50	50	49	49	49	50	48	48	48	49	46	45	46	45	43	46	46	45	49	50	47.6	.47

APPENDIX 5

Species Diversity And Evenness

Information content is often used as a measure of the diversity of many-species biological collections (Pielou 1966). Diversity is defined as the degree of uncertainty attached to the specific identity of any randomly selected individual (Pielou 1966). The greater the number of species and the more nearly equal their proportions, the greater the diversity (Pielou 1966).

For the present study, species diversity was measured by Brillouin's formula:

$$S.D. = \frac{1}{N} \log \frac{N!}{N_1!\, N_2! \cdots\cdots N_s!}$$

where:

N is the total number of individuals

s is the total number of species

N_1 is the total number of individuals in the 1th species

The diversity of a collection of species is maximum when the individuals are distributed as evenly as possible among the species. The ratio of the observed diversity to the maximum possible diversity is a measure of the evenness with which the individuals are divided among the species.